THE GLANDULOCAUDINE CHARACID FISHES OF THE GUAYAS BASIN IN WESTERN ECUADOR

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ABSTRACT. The Guayas basin on the Pacific coast of Ecuador has a small but remarkable fauna of Characidae, which includes three endemic glandulocaudines: *Landonia latidens* Eigenmann and Henn, 1914; *Phenacobrycon henni* (Eigenmann, 1914); and *Iotabrycon praecox,* a new genus and species described in this paper. The osteology of these glandulocaudines is described and compared with that of other characids in the Guayas basin. An attempt to find specialized osteological characters shared by the three glandulocaudine genera was unsuccessful. The osteological characters they share also occur in *Bryconamericus, Astyanax,* and probably many other generalized characids. Some remarks are made concerning the hooks found on the fin rays of many neotropical characids.
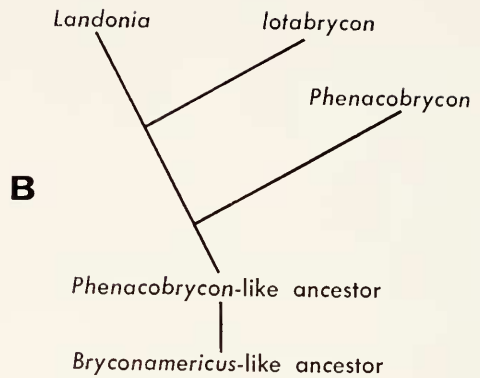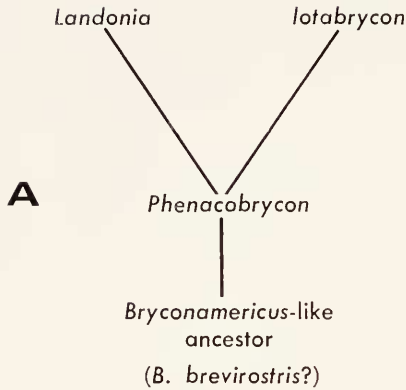
INTRODUCTION

The Glandulocaudinae are New World Characidae characterized by males having a variety of specialized structures (so-called "caudal glands") on the caudal fin and its base. The behavioral significance of these structures and of other peculiar secondary sexual characters, such as the spectacularly modified humeral scales in *Pterobrycon* (Bussing and Roberts, 1971), is still largely conjectural, despite recent studies on glandulocaudine behavior by Nelson (1964a, b, c).

Three monotypic glandulocaudine genera are relatively isolated in the Guayas basin on the Pacific coast of Ecuador. While differing considerably among themselves in dentition, osteology, general features, body proportions, etc., they are probably more closely related to each other than to any other glandulocaudines. They do not seem derived from the same stock as the geographically nearest trans-Andean glandulocaudines (*Pterobrycon, Gephyrocharax,* and *Argopleura*), which occur in the San Juan and Atrato drainages of Colombia, although a close relationship, especially to *Argopleura,* cannot be ruled out. No glandulocaudines occur on the Pacific coast of South America south of the Guayas basin, nor have any been found in the Esmeraldas, the large basin immediately north of the Guayas. One of the Guayas glandulocaudines (*Phenacobrycon*) has been reported from the Río Chone and the Río Puerto Viejo (Eigenmann et al., 1914), small rivers in the intervening coastal plain. The only other Characidae in the Guayas basin are three or four distinctive species of *Brycon,* two species of *Bryconamericus, Astyanax festae,* and an endemic species of *Hyphessobrycon* (*H. ecuadoriensis* Eigenmann and Henn). Eigenmann (1922) gives an account of the freshwater fishes of the Pacific slope of northwestern South America and their distribution. The two papers by Myers and Böhlke (1956) and Böhlke (1958) together constitute a review of the glandulocaudine genera, excluding *Saccoderma* and *Compsura,* which are placed in the Cheirodontinae, and *Brittanichthys,* subsequently described by Géry (1965).

Two of the Guayas glandulocaudines,

Landonia   Iotabrycon

A

Phenacobrycon

Bryconamericus-like
ancestor
(B. brevirostris?)

Landonia   Iotabrycon

Phenacobrycon

B

Phenacobrycon-like ancestor

Bryconamericus-like ancestor

Landonia Eigenmann and Henn, 1914 (*in* Eigenmann *et al.*, 1914) and *Phenacobrycon* Eigenmann, 1922, are already described. The third (*Iotabrycon*), which has the most specialized caudal gland of the three, is described here for the first time. An osteological study of these three genera was undertaken for the following reasons: 1) to permit a more precise diagnosis of the new genus; 2) to characterize more fully *Phenacobrycon* and *Landonia,* thus permitting their comparison with other characids; 3) to provide information about variation of osteological characters in Characidae, as background for other studies; and 4) to help in judging the utility of osteological comparisons for determining relationships among Characidae at the generic level.

The hypothesis is here investigated that the Guayas glandulocaudines are an autochthonous monophyletic lineage and had *Bryconamericus*-like ancestors, possibly similar to *Bryconamericus brevirostris* now inhabiting the Guayas basin. Diagram A represents one possible interpretation of their relationships. Another possible interpretation is shown in Diagram B.

The specimens upon which this paper is based were obtained during a survey to identify the principal freshwater food fishes of Ecuador for the International Center for Aquaculture of Auburn University, in October-December of 1971.

Collections in the Guayas basin were made by Sr. Fausto Silva M., Chief Fisheries Officer, and Sr. Gerinaldo Morales, both of the Departamento de Piscicultura of the Ministerio de la Producion of Ecuador; Mr. Ronnie J. Gilbert of Auburn University; and myself.

I wish to thank Dr. Stanley H. Weitzman, Division of Fishes, Smithsonian Institution, for helpful comments on the manuscript.

Note. Standard lengths are used throughout this paper, and all proportional measurements are expressed as times in standard length. All gill raker counts are made from alizarin preparations. It is practically impossible to make consistent gill raker counts in whole unstained specimens, and difficult to remove the first gill arch without leaving rakers behind. Also, rakers at the ends of the arch often show a sharp decrease in size, and the smallest rakers are often so small as to pass undetected unless stained by alizarin. Many published counts, especially for medium- and small-sized characids, err in giving too few rakers.

SYSTEMATIC ACCOUNT

PHENACOBRYCON Eigenmann, 1922

Phenacobrycon henni (Eigenmann)

Bryconamericus henni Eigenmann, 1914: 6 (*in* Eigenmann *et al.*, 1914; type locality = Vinces).
Phenacobrycon henni Eigenmann, 1922: 147

(*Bryconamericus henni* designated type species of monotypic new genus *Phenacobrycon*).— Eigenmann, 1927: 350–51 (synonymy, list of specimens, description), pl. 84, figs. 2, 3 (structures on caudal and anal fins of male); pl. 86, figs. 1–5 (full lateral view of male and female; dentition); pl. 97, fig. 7 (radiograph).

Material examined. MCZ 48660, 97 specimens, 21.4–33.0 mm, Río Vinces at Vinces, 5 November 1971; MCZ 48661, 56 specimens, 22.8–29.9 mm, isolated dry-season pool in Río Nuevo where it flows into left side of Río Vinces, one kilometer upstream from the town of Vinces, 5 November 1971; MCZ 48662, 9 specimens, 20.5–29.0 mm, Río Cristal 16 km E of Babahoyo, Los Ríos Province, 6 November 1971.

LANDONIA Eigenmann and Henn, 1914

Landonia latidens Eigenmann and Henn

Landonia latidens Eigenmann and Henn, 1914: 1 (*in* Eigenmann *et al.*, 1914; type locality= Vinces; *L. latidens* type of monotypic new genus *Landonia* by original designation).— Eigenmann, 1927: 400–401 (synonymy, list of specimens, description), pl. 77, figs. 1, 2, 4 (dentition); pl. 90, figs. 1, 2 (full lateral view of male and female).

Material examined. MCZ 48663, 14 specimens, 25.3–53.2 mm, Río Vinces at Vinces, 5 November 1971; MCZ 48664, 24 specimens, 23.9–42.1 mm, Río Cristal 16 km E of Babahoyo, Los Ríos Province, 6 November 1971.

IOTABRYCON new genus

Type species. *Iotabrycon praecox*, new species.

Diagnosis. Slender, minute glandulocaudine characids, body transparent in life except for opaque white peritoneum and sparsely distributed melanophores. Humeral spot absent. A small black spot at base of caudal fin present only in females. Dorsal fin ii, 7. Anal fin iii, 21 to v, 23. Pelvic fin 7. Adipose fin absent. Predorsum naked, body otherwise completely scaled. Anal fin scaleless. Lateral line incomplete, pore-bearing canals re-

stricted to the first few scales in the lateral series. Pseudotympanum absent. Premaxillary and dentary with a row of large conical teeth. Maxillary toothless. Caudal pouch of males supported by a single (?) large and characteristically modified scale on base of caudal fin, and a muscle not covered by scales extending over basal half of upper caudal fin lobe. A posteriorly directed process (indicated by an arrow in Fig. 3) appears to be separately ossified and may represent a second, highly modified, scale. Number of procurrent caudal rays equal in males and females; lower procurrent rays of males enlarged but otherwise unmodified. Hooks in males restricted to elongate anterior rays of anal fin and inner margin of pelvic fin rays. Rhinosphenoid bone present. Only three circumorbital bones. Vertebrae (precaudal + caudal exclusive of hypural complex) $17 + 18–19 = 35$ or 36.

Remarks. *Iotabrycon* is readily distinguished from *Phenacobrycon* and *Landonia* (which are probably its closest relatives) by its small size at maturity, caudal pouch structure, conical dentition, naked predorsum, absence of adipose fin, and fin ray counts. (See Table 1 and comparisons below.) There are several other minute or small glandulocaudines, but these are more deep-bodied, silvery with bluish reflections or brightly colored instead of transparent, and with completely different dentition. None of the described genera can be confused with *Iotabrycon*, although some share with it such characters as lack of adipose fin (*Pterobrycon landoni*, *Corynopoma*, undescribed *Tyttocharax* from Ecuadorean Amazon), incomplete lateral line (*Glandulocauda*, *Mimagoniates*), incomplete circumorbital series (*Tyttocharax*), presence of rhinosphenoid bone (*Tyttocharax*). A single row of conical teeth on premaxillary and dentary is found in *Brittanichthys*, but its teeth are minute and relatively numerous. A "naked" muscle extending well onto the upper caudal fin lobe in males apparently occurs only in *Iotabrycon*.
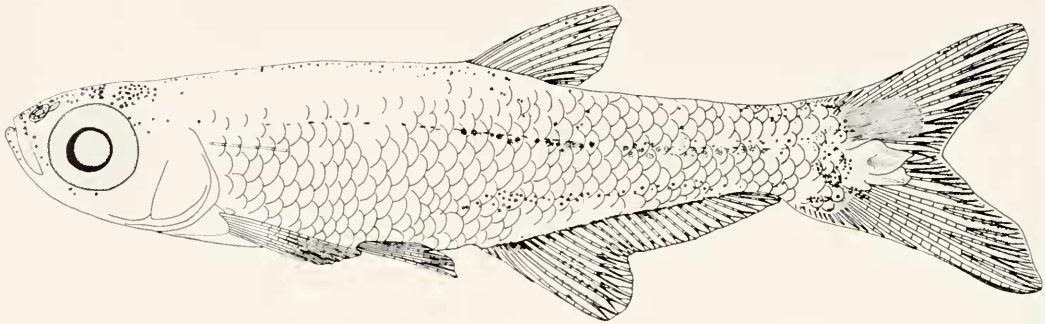
Figure 1. *lotabrycon praecox*, new genus and new species, MCZ 48659, 17.9-mm ♂ paratype (hooks on anal fin based on alizarin preparation of 18.8-mm ♂ paratype).

Iotabrycon praecox new species
Figures 1–4

Holotype. MCZ 48658, a male 18.6 mm, from an isolated dry season pool in Río Nuevo where it flows into left side of Río Vinces, one kilometer upstream from the town of Vinces, 5 November 1971.

Paratypes. MCZ 48659, 8 females or immatures 16.2–19.9 mm and 12 males 17.2–18.8 mm, collected with the holotype.

General features. Largest specimen, a female, 19.9 mm. Largest male 18.8 mm. Males as small as 17.4 mm sexually mature (as indicated by full development of caudal gland and hooks on anal and pelvic fins). Body elongate, slender. Eye large. Adipose eyelid absent. Mouth moderately superior, lower jaw slightly projecting. Maxillary extending to anterior border of eye but not beyond, exposed (not slipping under first infraorbital, which is greatly reduced); leading edge of maxillary convex. Premaxillary with a row of 5 or 6 conical teeth; maxillary toothless; dentary with a row of 6 teeth, first four somewhat larger than those on premaxillary, last two reduced; first tooth on dentary pointed into mouth, second tooth pointed outwards (Fig. 11). First gill arch with 5 or 6 + 12 moderately long, edentulous, widely spaced gill rakers (Fig. 19). Pseudotympanum absent, area normally occupied by pseudotympanum with orangish fat deposits. Belly rounded. No membranous ventral keel between pelvic fins and anal fin origin (often present in minute or larval characids at comparable sizes).

Proportional measurements. The measurements of the holotype are given first, followed in parentheses by the ranges in the type series. Body depth 4.4(4.1–4.8). Depth caudal peduncle 9.3(9.3–11.3). Predorsal length 1.8(1.7–1.9). Preanal length 1.7(1.7–1.8). Prepelvic length 2.3(2.2–2.5). Length anal base 3.4(3.2–3.6). Height dorsal fin 5.3(4.3–5.4). Height anal fin 5.6(4.5–6.2). Length pectoral fin 5.3(5.0–6.3). Length pelvic fin 7.2(6.9–9.7). Length upper caudal fin lobe 3.6(3.4–4.4). Length lower caudal fin lobe 3.3(3.1–4.0). Head length 4.1(3.9–4.3). Length of orbit 10.3(9.5–11.2).

Fins. Dorsal fin rays ii, 7 (ii, 6 in one specimen). Anal fin rays iv, 21 to v, 23 (one specimen with iv, 24 has an abnormally thin 23rd ray). Principal caudal fin rays 10 + 9. Procurrent caudal rays: 13 upper + 12 lower (18.8-mm ♂); 13 + 13 (17.4-mm ♀); 11 + 11 (16.2-mm immature). Pectoral fin rays usually 9 or 10. Pelvic fin rays 7. Adipose fin absent.

Dorsal fin origin slightly in front of a vertical line through anal fin origin, and predorsal length shorter than preanal length, in all specimens with ii, 7 dorsal fin rays. In unique specimen with ii, 6 dorsal fin rays, the dorsal fin origin slightly posterior to anal fin origin; its predorsal

Figure 2.   Caudal gland of 17.9-mm ♂ *Iotabrycon praecox*.

length (1.75) slightly greater than its preanal length (1.8). Tip of pectoral fin extends beyond pelvic fin origin. Caudal fin relatively large, lower lobe slightly larger than upper lobe, possibly less so in females. Fins scaleless, except for modified scale on base of caudal fin in sexually mature males.

Squamation. Nape and predorsal region naked, scaleless area corresponding to two–three full scale rows on either side (Fig. 1). Scales in a lateral series 38–40. Scale counts difficult to make. In four specimens stained with Delafield's hematoxylin, which makes scale pockets show up well, scale counts 38(2) and 39(2). Lateral line incomplete, only 3–6 anteriormost scales in lateral series bearing pores. A 16.8-mm

specimen has 4 weakly developed pores. In a 16.4-mm specimen pores undeveloped. Smallest specimen, 16.2-mm, stained in alizarin, with 5 scales bearing pores.

Sexual dimorphism. Mature males readily distinguished from immature specimens and females by specialized structures on caudal fin, described below. Caudal fin larger in males: length of upper caudal lobe 3.4–3.7 (average 3.6) in males, 3.5–4.4 (average 3.9) in females; length of lower caudal lobe 3.1–3.5 (average 3.3) in males, 3.3–3.9 (average 3.6) in females. In both sexes lower caudal lobe about ten percent longer than upper. Lower procurrent caudal rays relatively larger in males, giving lower margin of caudal base a keel-like structure. In males caudal peduncle
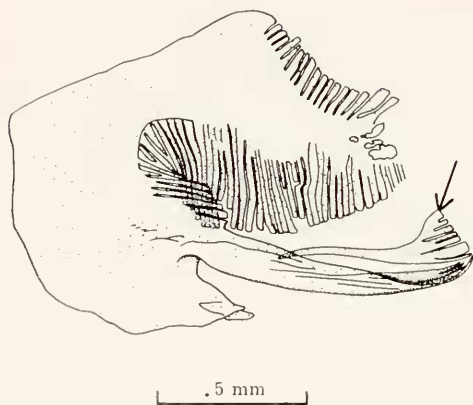
Figure 3. Modified scale in caudal gland of 18.8-mm ♂ *Iotabrycon praecox* (drawn from an alizarin preparation). Arrow points to separately ossified process which may represent a second modified scale.

Figure 4. Left pelvic fin and girdle of 18.8-mm ♂ *Iotabrycon praecox*, showing distribution of hooks on fin rays (ventral view).

depth (range 9.3–10.8, average 9.9) tends to be greater than in females and immature specimens (range 9.4–11.3, average 10.5). In males the first eight or nine segmented anal fin rays bear hooks and form a distinct lobe; pelvic fins relatively longer and bearing hooks; pelvic fin length 6.9–8.0, (average 7.4). In females anal and pelvic fins hookless; pelvic length 8.5–9.7, average 9.0. No other evident differences in proportional measurements between sexes.

Of 12 male specimens in the type series, the six largest individuals range from 18.0–18.8 mm standard length, whereas out of only 8 females and immatures, the largest female, at 19.9 mm, is considerably larger.

Modified caudal structures in males (Figs. 1–3). Twelve of the 20 specimens in the type series are identified as males because they bear well-developed hooks on the anal and pelvic fins and have a "caudal gland." In *Iotabrycon* the caudal modifications consist of a highly modified scale supporting a large caudal pouch and a muscle with extensive attachments to the proximal half of the upper caudal lobe. The modified scales on opposite sides of the caudal fin are mirror images. It is questionable whether the posteriorly directed process indicated by an arrow in
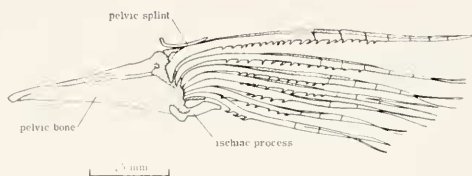
Figure 3 represents a separate scale. They are well developed and of similar morphology in all the males in the type series. The principal caudal rays are unmodified, except in size, the caudal fin being somewhat larger in males than in females. The upper procurrent caudal rays in males are unmodified but the lower procurrent rays are considerably enlarged, giving the lower margin of the male caudal fin a keel-like appearance.

Comparisons with *Phenacobrycon* and *Landonia* (Table 1)

Some comparisons between *Iotabrycon*, *Phenacobrycon*, and *Landonia* appear in Table 1. The smallest *Phenacobrycon* examined, 20.5–24.0 mm, are readily distinguished from *Iotabrycon* by their coloration; deeper body (depth of body normally 3.1–3.3; body depth of 20.5-mm specimen 3.8, but it is emaciated); adipose fin; higher dorsal, anal, and pelvic fin ray counts; dentition; and lack of sexual dimorphism. Most of these differences should also serve to differentiate specimens of *Phenacobrycon* of the same size as *Iotabrycon*. Very young *Landonia* should be readily distinguished by their higher scale and fin ray counts, adipose fin, and lack of sexual dimorphism.

Coloration. Live *Phenacobrycon* and *Landonia* have the same coloration: silvery overall, with bluish reflections; no humeral spot; upper lobe of caudal fin pale lemon yellow with its distal margin black, lower lobe of caudal usually clear; dorsal fin dusky, especially near tip; other fins clear.

In some specimens of *Phenacobrycon* the lower caudal lobe is also yellow and tipped with black, but the coloration is always more intense on the upper lobe. Preserved specimens exhibit a small oblong spot in the middle of the caudal fin base; fine melanophores occur on the tip of the dorsal fin, paralleling the anal fin base and the posterior half of the horizontal septum, and scattered on the dorsum. In live *Iotabrycon* the body is translucent except for the opaque white peritoneum; the "caudal gland" area of males is less translucent than the corresponding area in females. None of the Guayas glandulocaudines has a lateral silvery band, although all have a concentration of melanophores forming a thin black line along the posterior two-thirds of the horizontal septum. A broad, sharply demarcated, silver lateral band is a constant character of *Argopleura*.

Dentition. In *Phenacobrycon* (Fig. 5) the premaxillary bears two rows of sharp-pointed multicuspid teeth in which the central cusp is enlarged: the external premaxillary row of three tricuspid teeth, the
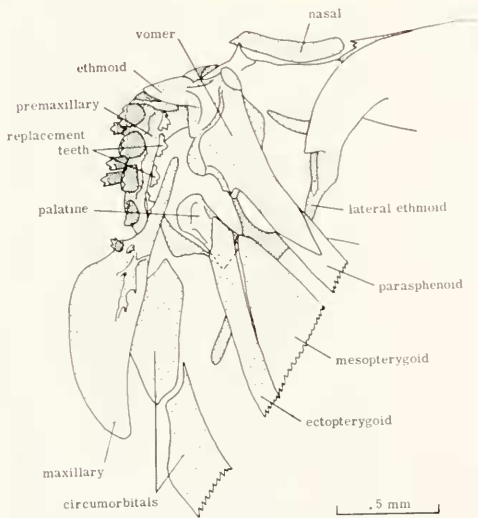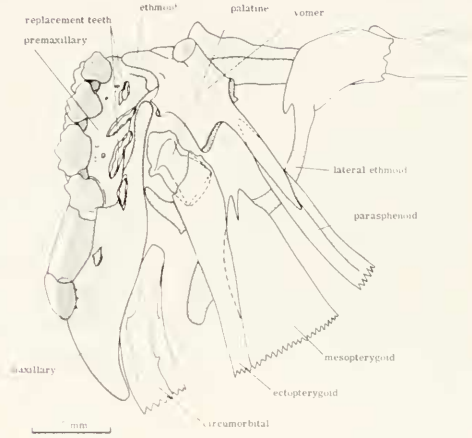

Figure 6. *Landonia latidens*. Upper jaw (left side removed), and anterior portion of palate (ventral-oblique view of 32.1-mm specimen).

internal row of four teeth each with four or five cusps. The dentary bears a single row of four large quinquicuspid teeth with enlarged central cusp followed by two very small conical teeth. The maxillary bears a single small tricuspid tooth.

In *Landonia* (Fig. 6) the premaxillary bears two irregular rows of multicuspid teeth in which the cusps are about equal in size and have rounded crowns even in newly formed teeth. The external row has three tricuspid teeth, the internal row four quinquicuspid teeth. The dentary bears five or six teeth, the first two or three each with five rounded cusps, the last two or three with a straight cutting edge without any trace of cusps. The maxillary bears two or three large elongate subrectangular teeth with straight cutting edges similar to the posteriormost two dentary teeth. Alizarin preparations of the replacement teeth of the maxillary fail to reveal separately formed cusps or fusion of conical elements in their formation. No other genus of Characidae has teeth similar to *Landonia*.

Caudal glands. In *Landonia* the caudal pouch is membranous; the terminal scale in the pored lateral line series (Fig. 26) is dorsoventrally expanded but does not

Figure 5. *Phenacobrycon henni*. Upper jaw (left side removed), and anterior portion of palate (ventral-oblique view of 25.6-mm specimen).

TABLE 1. SOME MORPHOLOGICAL AND OSTEOLOGICAL CHARACTERS IN *IOTABRYCON*, *PHENACOBRYCON*, AND *LANDONIA*. P = PRIMITIVE, R = REDUCTIVE, L = LABILE, S = SPECIALIZED; SEE TEXT FOR EXPLANATION.

	Iotabrycon	Phenacobrycon	Landonia
1. Dorsal fin	ii, 7 R, L	ii, 8 P	ii, 8 P
2. Adipose fin	absent R	present P	present P
3. Anal fin	iii, 21 to v, 23 L	v, 27 to vi, 29 L	v, 29 to vi, 30 L
4. Pectoral fin	8 or 9 (16.2 mm) 10 (18.8 mm) R, L	11 or 12 P	11 P
5. Postcleithra	2, 3 R 3 slender for its entire length R	1, 2, 3 P 1 and 2 widely separated, 3 with a proximal laminar portion P	1, 2, 3 P 1 and 2 widely separated, 3 with a proximal laminar portion P
6. Pelvic fin	7 S, R	8 P	8 P
7. Procurrent caudal rays	11 + 11 (16.2 mm) 13 + 12 (18.8 mm) 13 + 13 (17.4 mm) lower procurrent rays enlarged in males, producing a keel S, L	9 + 8 (27.1 and 27.7 mm) 10 + 8 (25.5 mm) lower procurrent rays not enlarged in males? P	12 + 10 (25.6 mm) 13 + 10 (31.0 mm) 13 + 12 (30.4 mm) 14 + 11 (42.1 mm) 14 + 12 (32.1 mm) lower procurrent rays not enlarged in males P
8. Caudal pouch	supported internally by highly modified caudal scale S	membranous S, L?	membranous S, L?
9. Extensive muscle to upper lobe of caudal fin in males	present S	absent P	absent P
10. Epurals	2 P, L	2 P, L	2 P, L
11. Lateral line scale count	38–40 L	37–38 L	45–50 L
12. Pored lateral line scales	3–6 anteriormost scales only R	complete P	complete P
13. Extent of squamation on body	predorsal area naked, rest of body completely scaled R	body completely scaled P	body completely scaled P

Table 1. (Continued)

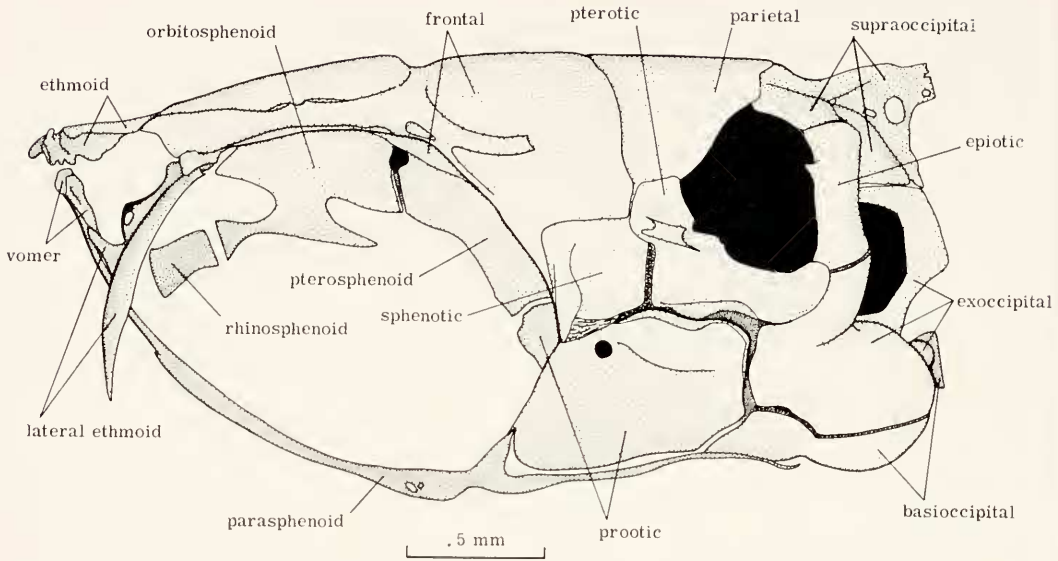|	Iotabrycon	Phenacobrycon	Landonia
14. Scales on anal fin	anal fin naked R	base of anal fin with a row of scales for its entire length L	only anterior one-third of anal base with a row of scales L
15. Teeth on premaxillary	single row of 5–6 conical teeth R	outer row of 3 and inner row of 4 tricuspid teeth with sharp points P	outer row of 3 and inner row of 4 tricuspid teeth with points somewhat rounded S
16. Teeth on maxillary	none R	a single small tricuspid tooth at juncture with premaxillary L	two large straight-edged teeth forming a continuous cutting edge for two-thirds of distal portion of maxillary S
17. Teeth on dentary	single row of 6 conical teeth (last 2 teeth reduced in size) S?, R	single row of 3 large quinquicuspid teeth with sharp points and 2 small (conical?) teeth P	single row of 2 or 3 multicuspid (quinquicuspid?) teeth with rounded points and 2 or 3 large straight-edged teeth S
18. Mode of tooth replacement	at seemingly irregular intervals along tooth rows R	alternating replacement from one side of jaws to the other P	"simultaneous" replacement of all jaw teeth at once S
19. Gill rakers	3 or 4 + 11 (16.2 mm) / 5 + 11 or 12 (18.8 mm) R, L	11 or 12 + 17 / 13 + 21 P, L	9 + 19 (42.1 mm) / 10 + 18 (25.6 mm) / 12 + 18 (32.1 mm) P, L
20. Number of basibranchials	4 P	4 P	4 P
21. Supraorbital	absent R	absent R	absent R
22. Circumorbitals	1, 2, 3 R	1, 2, 3, 4, 5, 6 P	1 + 2, 3 + 4, 5, 6 S
23. Rhinosphenoid	present L?	absent R?	absent R?
24. Posterior portion of parasphenoid	weakly developed R	strongly developed P	strongly developed P
25. Supraneurals	5–6 P	6–7 P	6 P
26. Vertebrae	17 + 18 – 19 P?, L?	16 + 18 P?, L?	16 + 19 – 20 P, L?

Figure 7. *Iotabrycon praecox.* Lateral view of cranium (18.8-mm specimen).

enter into the construction of the pouch (Eigenmann, 1927, pl. 84, fig. 2; Nelson, 1964a, fig. 46 on p. 72). *Phenacobrycon* (Nelson, 1964a, fig. 36 on p. 71) has a membranous pouch perhaps less well developed than in *Landonia*, and some slightly modified scales on the ventral half of the caudal base. The last pored scale in the lateral line is the same size as the ones preceding (i.e., it is not expanded).

Distribution of hooks on anal and pelvic fin rays. In the Guayas glandulocaudines the hooks characteristic of mature males occur on the anal and pelvic fins (most if not all glandulocaudines have hooks on the anal fin; many also have hooks on the caudal fin; and some may lack hooks on the pelvics).

In *Phenacobrycon* hooks occur on the rays in the anterior and posterior portions of the anal fin but not on the rays in between. According to Eigenmann (1927: 401) the first ten and the last ten "developed" rays of the anal fin of males bear hooks. In the single male specimen collected in November 1971 (MCZ 48660, 28.2 mm), the anterior portion of the anal fin

has two rudimentary hooks on the last unbranched ray, one hook on the first and second branched rays, two hooks on the third branched ray, one hook on the fourth branched ray, and two hooks on the fifth to eighth branched rays. The posterior portion of the anal fin has two hooks on the 23rd, 24th, and 26th to 28th branched rays and three hooks on the 25th. The ninth through 22nd branched rays are without hooks. In *Landonia*, as in *Iotabrycon*, hooks are restricted to the anterior portion of the anal fin. Eigenmann (1927: 350) reported *Landonia* with several "tubercles" on the second, third and fourth rays and a large retrorse hook on the fifth through ninth rays. In all male *Landonia* collected in November 1971, the hooks are likewise restricted to the anterior portion of the anal fin. In the specimen with the greatest development of hooks (MCZ 48664, 38.8 mm) the last undivided ray and first branched ray bear two hooks and the second through sixth branched rays bear a single hook.

The distribution of hooks on the pelvic fin rays differs in the three genera. In

Figure 8. *Phenacobrycon henni.* Lateral view of cranium (27.7-mm specimen).

Iotabrycon hooks occur on all of the pelvic rays but are medially directed and restricted to the inner edge of each ray (Fig. 4). In *Phenacobrycon* and *Landonia* the outermost pelvic ray has no hooks. In *Landonia* the hooks are medially directed and restricted to the inner edge of each ray as in *Iotabrycon*, but in *Phenacobrycon* the hooks are dorsally directed and occur on all branches of each ray, as in *Bryconamericus scleroparius.*

Replacement teeth and tooth replacement. In *Iotabrycon*, as in other minute characins with conical teeth, the replacement teeth are in varying stages of development. In adults of *Phenacobrycon* and *Landonia*, as in other characids with multicuspid teeth, all of the replacement teeth on one side of both the upper and lower jaws are always in the same stage of formation, and at least in *Phenacobrycon* all the teeth on one side of the jaws are probably replaced in one continuous process; in other words there is nearly simultaneous replacement of one-half of the entire dentition, first on one side, then on the other side of the jaws, as occurs in

Brycon and other characids with multicuspid teeth (Roberts, 1967). In a population sample of 97 *Phenacobrycon* (MCZ 48660) are 85 specimens in which all of the teeth are in functional position on both sides of the jaws, and 12 specimens in which the teeth on only one side of the jaws are in the process of replacement.

In *Iotabrycon* the replacement teeth in both jaws lie in the gum just inside the row of functional teeth. In *Phenacobrycon* the replacement teeth for the internal row of teeth on the premaxillary and for the single small tooth on the maxillary lie simply in the gum (Fig. 5), but the replacement teeth for the external premaxillary tooth row are entirely enclosed within the premaxillary bone, and the replacement teeth for the lower jaw are almost entirely enclosed in the dentary, that is, they lie in a deep trench in the medial face of the dentary—as in *Alestes* (Roberts, 1967, fig. 3 on p. 246). In *Landonia* only the internal row of replacement teeth on the premaxillary lies superficially in the gum; the replacement teeth for the external row on the premaxillary, for the maxillary, and
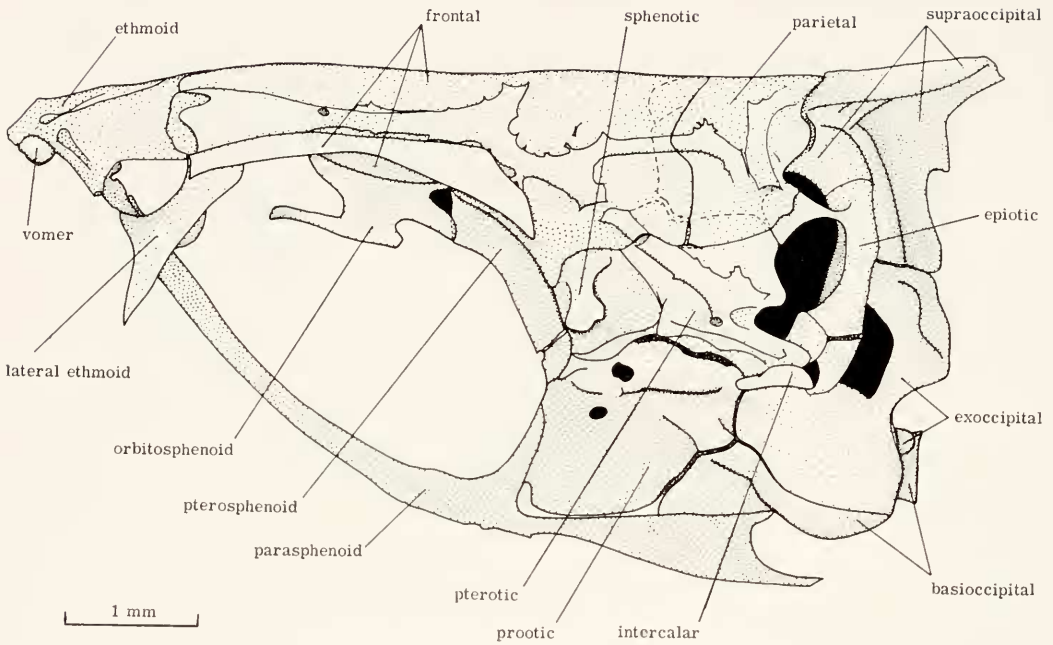
ethmoid frontal sphenotic parietal supraoccipital

epiotic

vomer

lateral ethmoid

orbitosphenoid

pterosphenoid

parasphenoid

exoccipital

basioccipital

pterotic

prootic intercalar

1 mm

Figure 9. *Landonia latidens.* Lateral view of cranium (42.1-mm specimen).

for the dentary are entirely enclosed within these bones (Figs. 6, 15).

In the multicuspid teeth of *Phenacobrycon* and *Landonia* each cusp represents a separately formed conical element. In the formation of the peculiar straight-edged teeth of *Landonia*, however, there is no sign of separate conical elements, at least not in alizarin preparations. When these teeth first show signs of ossification they have already acquired a perfectly straight-edged crown.

After examining five alizarin preparations of *Landonia*, I am inclined to think that all of the teeth on both sides of its jaws are replaced in one continuous and relatively rapid ("simultaneous") act. The reasons are: 1) in none of the specimens does there appear to be differential wear of the teeth on one side of the jaws, nor do the teeth on one side of the jaws differ in any other way (such as coloration, density of alizarin uptake) from those on the other side, as one would expect to find in a characid with replacement alternating from side to side; 2) in four of the five specimens the replacement teeth (note: the replacement teeth enclosed in their respective bones are visible through the bone, and the replacement teeth for the internal row on the premaxillary lie exposed in the gum) on both sides of the jaw are in the same stage of formation; and 3) in the remaining specimen, 31.0 mm, there are no ossified replacement teeth on either side of the jaws and the functional teeth appear unworn and newly arrived in position. Finally, in a population sample of 24 *Landonia* (MCZ 48664), there are 23 specimens in which all of the teeth on both sides of the jaws are firmly in functional position, and one specimen in which the gums are uniformly soft and swollen, and the teeth, which are easily movable in the soft tissue, are in the process of coming into functional position on both sides of the jaws.
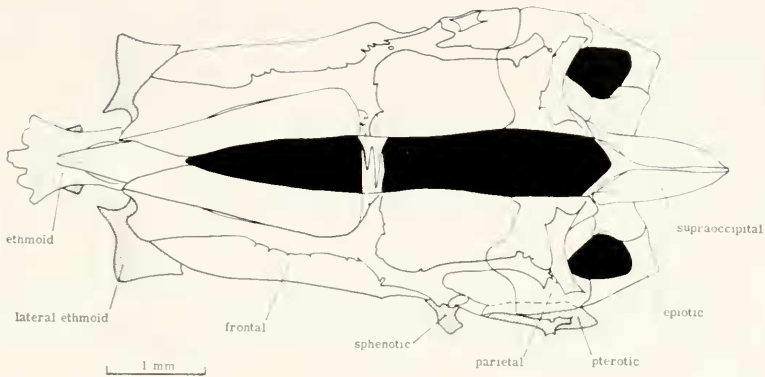
Size. Eigenmann *et al.* (1914) and

Figure 10. *Landonia latidens*. Dorsal view of cranium (42.1-mm specimen).

Eigenmann (1922) reported *Phenacobrycon henni* from 46 to 53 mm and *Landonia latidens* from 28 to 59 mm (total length?). In the material collected by Silva, Gilbert, and myself in 1971 *Phenacobrycon* are from 20.5 to 33.0 mm in standard length, and the *Landonia* significantly larger, from 23.9 to 53.2 mm in standard length. In both *Phenacobrycon* and *Landonia* (and probably in *Iotabrycon*) the largest specimens in a population are females. Males with sexually dimorphic characters fully developed are known from 28.2 mm (MCZ 48660) to 50 mm (total length?) in

Phenacobrycon and from 36.1–42.1 mm (MCZ 48664) to 50 mm (total length?) in *Landonia.* It may be recalled that the largest specimen of *Iotabrycon* is a 19.9-mm female, the males ranging from 17.2 to 18.8 mm.

ECOLOGY

Habitat. *Iotabrycon* was found in a single locality: a large, isolated dry-season pool in the Río Nuevo a few hundred yards from where it flows into the Río Vinces. A shaded arm of this pool, about 5 meters
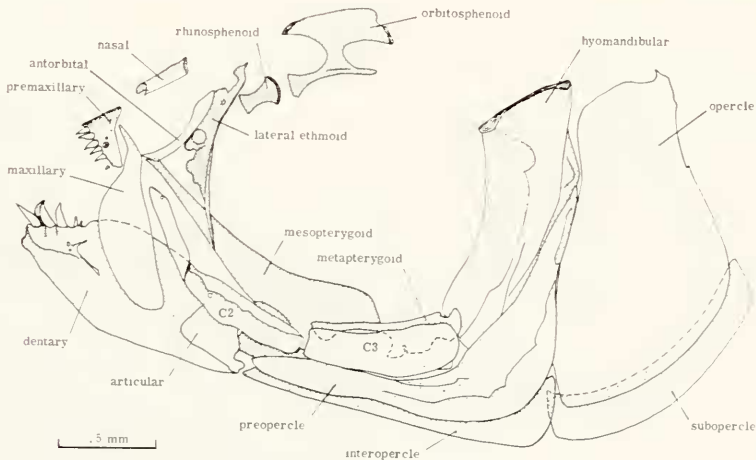

Figure 11. *Iotabrycon praecox*. Lateral view of jaws, suspensorium, and facial bones (17.4-mm specimen; teeth in lower jaw drawn from 18.8-mm specimen).
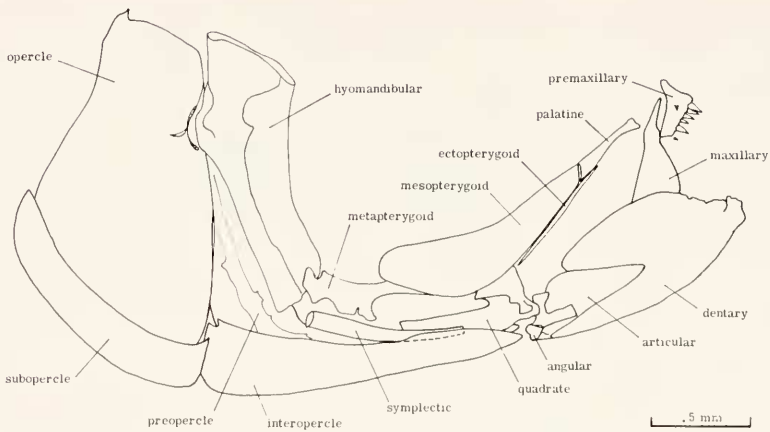
Figure 12. *Iotabrycon praecox.* Internal view of jaws, suspensorium, and facial bones (circumorbitols removed; teeth in lower jaw inadvertently dislodged) (17.4-mm specimen).

wide, 50 meters long, and no more than a meter deep, was rotenoned in the late afternoon on 5 November 1971, at which time the water temperature in the pool was 78°F. It contained a good proportion of the species found in all but the deepest and swiftest waters of the nearby Río Vinces, including: *Hoplias microlepis, Lebiasina bimaculata, Astyanax festae, Brycon alburnus, Bryconamericus brevirostris, Phenacobrycon henni,* young *Rhoadsia altipinna,* *Leporinus ecuadoriensis, Curimatorbis troscheli, Ichthyoelephas humeralis,* a large *Sternopygus macrurus, Pimelodella,* young *Plecostomus spinosissimus, Pseudopoecilia, Aequidens rivulatus,* and *Cichlaurus festae. Landonia* was found only in backwaters of the Río Vinces and Río Cristal, where they are respectively perhaps 100 meters and 50 meters wide. *Phenacobrycon* were taken at the same localities, and also in the isolated pool with *Iotabrycon.*
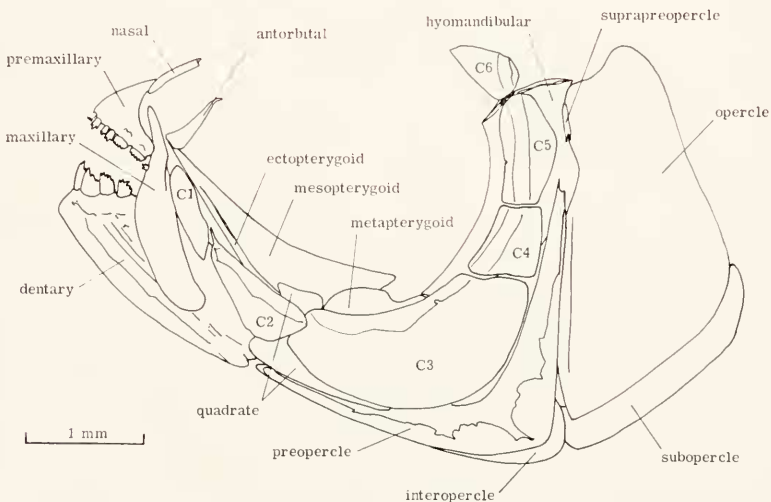

Figure 13. *Phenacobrycon henni.* Lateral view of jaws, suspensorium, and facial bones (27.1-mm specimen).
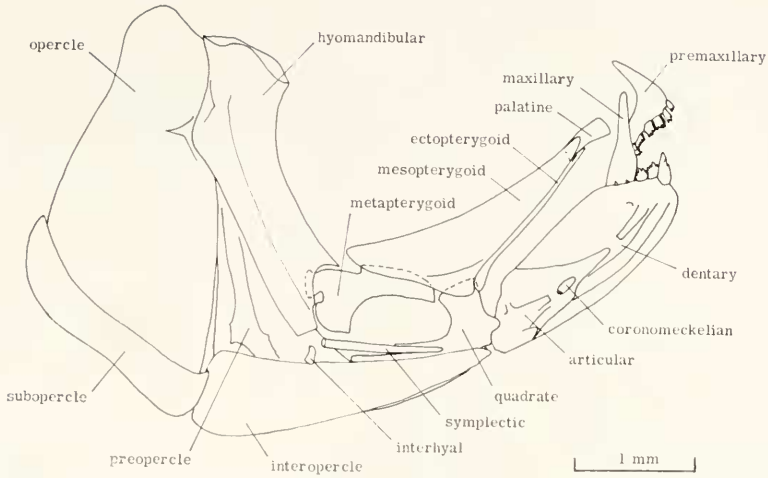
Figure 14. *Phenacobrycon henni*. Internal view of jaws, suspensorium, and facial bones (27.1-mm specimen).

Relative abundance. During our field-work in 1971 glandulocaudines were found only in large, low gradient streams of the Guayas basin, unlike the ubiquitous and more common *Bryconamericus brevirostris* and *Astyanax festae*. Of the three glandulo-caudine genera, *Phenacobrycon* is by far the commonest in our samples. A preponderance of *Phenacobrycon* over *Landonia* also is found in the only other two recorded collections: the Festa collection from the Río Vinces, made sometime before

1895, contains 67 *Phenacobrycon* and 5 *Landonia* (reported in Tortonese, 1941-42). In 1913 Henn obtained 15 *Landonia* and more than 40 *Phenacobrycon* at Vinces, and 22 *Landonia* and "many" *Phenacobrycon* at Colimes on the Río Daule (Eigenmann, 1927).

Feeding habits. The specimens of *Iotabrycon*, *Phenacobrycon*, and *Landonia* taken near Vinces in November 1971 appear to be well fed, in contrast to *Bryconamericus brevirostris* and *Astyanax*
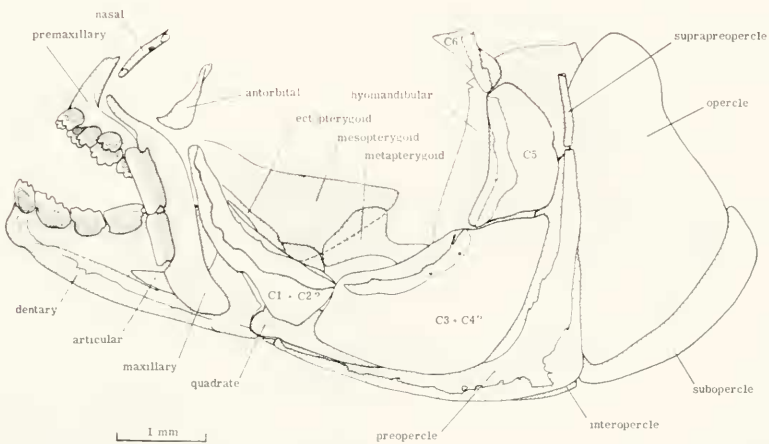

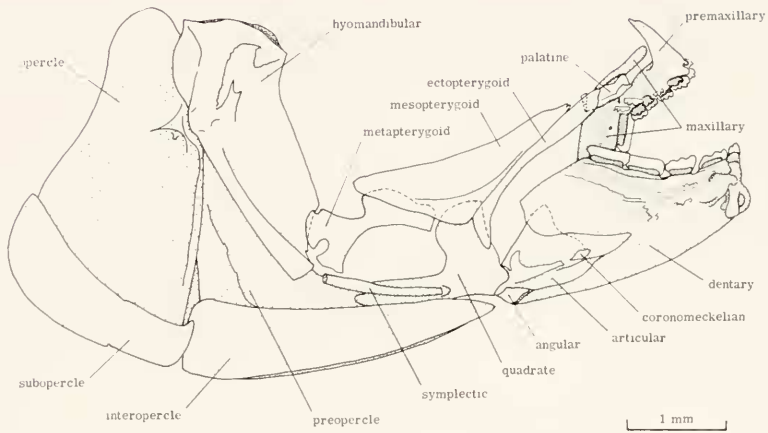Figure 15. *Landonia latidens*. Lateral view of jaws, suspensorium, and facial bones (32.1-mm specimen).

Figure 16. *Landonia latidens.* Internal view of jaws, suspensorium, and facial bones (32.1-mm specimen).

festae, many of which were taken in starved condition. Many specimens of *Bryconamericus* have guts full of mud. Several *Landonia* had empty guts. A 36.1-mm *Landonia* had a well-formed bolus of segmented fin rays, perhaps from a characid, and nothing else. The stomach of a 42.0-mm specimen contained a packet of about 24 characid scales from 1.7 to 3.0 mm in their longest dimension, including some 2.2-mm scales which appear identical to scales on a 53-mm *Astyanax festae* from the same collection. Its own scales are 1.2 mm in their longest dimension. A 31.8-mm specimen contained a few scales and a few strands of what looked like a filamentous alga. None of the *Landonia* examined had ingested insects or sand and soil particles.

In contrast to *Landonia, Phenacobrycon* feed largely on an assortment of Arthropoda. A list of the arthropod stomach contents of ten *Phenacobrycon* from the Río Vinces (MCZ 48660) was kindly prepared by Dr. John Lawrence:

Araneida	2
Acarina	1
Collembola	20+
Orthoptera	
Tridactylidae	2
Hemiptera	
Gerridae	14+
Diptera	
3 kinds of larvae	7+
Hymenoptera	1
Coleoptera	
Staphylinidae	1
Limnichidae	1

The waterstriders, almost certainly taken alive at the surface, and the springtails, possibly taken at the surface, are the predominant food items. The waterstriders constitute the item with greatest biomass among the stomach contents. The Tridactylidae are minute mole crickets which tend to live in damp soil at or near the water's edge. The staphylinid beetle, mite (a terrestrial form), hymenopteran, and perhaps the spiders are likely to have been taken while floating or sinking after falling onto the water's surface. The dipteran larvae are almost certainly taken at the bottom. Along with the arthropods one finds sand and soil particles, usually held together in a flocculent mass, presumably ingested from the bottom, and a quantity of very small, brown oval objects that might be seeds, but no fish scales or fin rays.

Ten *Phenacobrycon* from this same population sample had tooth replacement in progress. The stomachs of several of
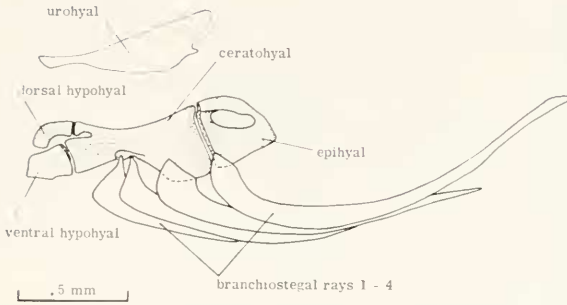
Figure 17. *Iotabrycon praecox.* Lateral view of left half of hyoid arch (minus basihyal and interhyal) and urohyal (offset) (18.8-mm specimen).

these specimens are relatively empty, an indication that they had stopped feeding.

The stomach contents of *Iotabrycon* have not been investigated, in order to conserve specimens.

OSTEOLOGY
Figures 4–26; Tables 1, 2

Osteological study material. This account is based on the following material:

Iotabrycon praecox: MCZ 48659, 3 paratypes: 16.2-mm immature; 17.4-mm female; 18.8-mm male.

Phenacobrycon henni: MCZ 48661, 3 specimens, 25.6–27.7 mm.

Landonia latidens: MCZ 48664, 5 specimens, 25.6–42.1 mm.

Bryconamericus brevirostris: MCZ 48665, 2 specimens, 51.7 and 60.5 mm, Río Vinces at Vinces, 5 November 1971.

Bryconamericus scleroparius: MCZ 48666, 5 specimens, 31.9–39.7 mm, Arroyo Campo Triste, tributary to Río Blanco, Esmeraldas basin, 27 km NW of town of Santo Domingo, 20 October 1971.

Astyanax festae: MCZ 48667, 3 specimens, 34.5–46.5 mm, Río Vinces at Vinces, 5 November 1971.

Brycon dentex: MCZ 48668, 2 specimens, 79.0 and 82.0 mm, Río Esmeraldas 35 km upstream from city of Esmeraldas, 21 October 1971.

Cranium (Figs. 7–10). Crania of *Phenacobrycon* (Fig. 8) and *Landonia* (Figs. 9, 10) are similar to each other except in the ethmoid region. Both lack rhinosphenoids and the strong ventroposteriorly directed pterotic process found in *Brycon,* but otherwise differ little from that genus. The

posterior half of the cranium of *Landonia* is slightly foreshortened and deeper, as evidenced in the shapes of the parietal, pterotic, and prootic bones, and in the approximation of the parietal branch of the frontal laterosensory canal to the parietal laterosensory canal. In *Phenacobrycon* the ethmoid region is similar to that in *Brycon* in that the vomer remains separate from the ethmoid, and the vomerine process of the lateral ethmoid is in intimate contact with the vomer. In *Landonia* ethmoid and vomer are fused but the vomerine processes of the lateral ethmoids are weakly developed and fail to contact the vomer. The lateral portion of the lateral ethmoid also is relatively smaller in *Landonia.*

Dorsal cranial fontanel and epiphyseal bar well developed in all three genera. In *Iotabrycon* posterior portion of cranial fontanel about 1½ times as long as anterior portion, anterior portion slightly wider than posterior portion. In *Phenacobrycon* posterior and anterior portions of cranial fontanel about equal in length and width. In *Landonia* anterior portion slightly shorter and narrower than posterior portion (Fig. 10). Despite these slight differences in proportion between the anterior and posterior portions, the shape of the cranial fontanel is very similar in the three genera.

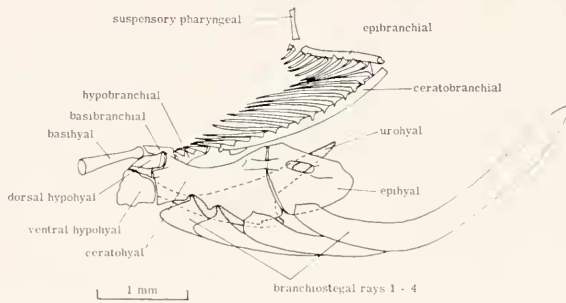The cranium of *Iotabrycon* (Fig. 7) differs most notably from crania of

Figure 18. *Landonia latidens.* Lateral view of left half of hyoid (minus interhyal) and first gill arches (32.1-mm specimen).

Phenacobrycon and *Landonia* in possessing a well-developed rhinosphenoid. The relationships of ethmoid, vomer, and lateral ethmoid are as in *Phenacobrycon.* In *Landonia* and *Phenacobrycon* the posteriormost part of the parasphenoid provides a strong, ventrally directed, keel-like structure on the base of the cranium; in *Iotabrycon* the posterior part of the parasphenoid is weakly developed, flattened from side to side, and fails to form a strong ventral keel.

In *Iotabrycon* only the frontal and

pterotic branches of the cephalic laterosensory system develop bony canals. The pterotic canal is short, and the frontal canal fails to develop a parietal branch. Parietal canal absent.

In all three genera the ventral part of the orbitosphenoid has a posteriorly directed process. This process is relatively weak in *Landonia.*

In *Phenacobrycon* and *Iotabrycon* the vertical laminar portion of the supraoccipital is fenestrated.
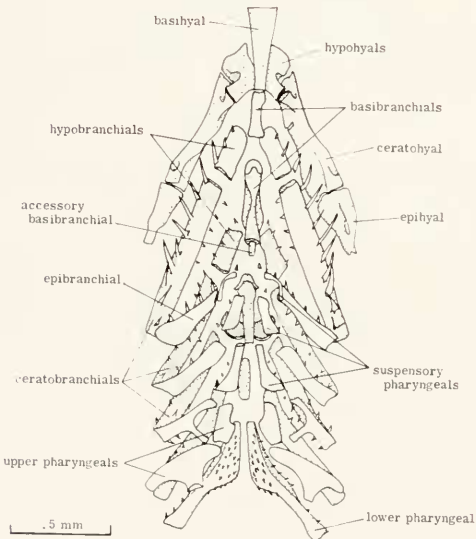

Figure 19. *Iotabrycon praecox.* Dorsal view of hyoid (minus interhyal) and gill arches (branchiostegal rays removed) (18.8-mm specimen).
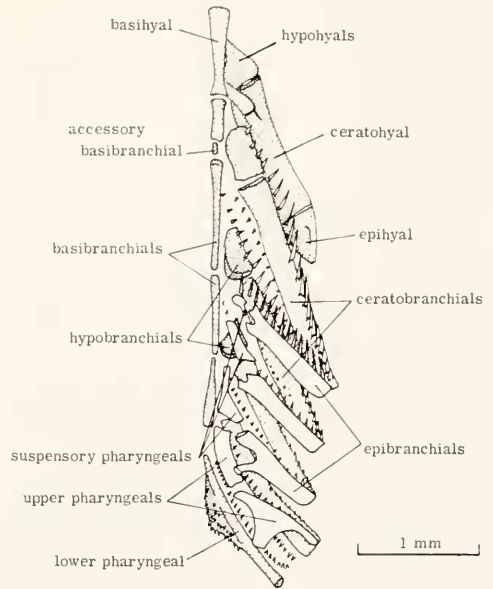

Figure 20. *Phenacobrycon henni.* Dorsal view of right half of hyoid (minus interhyal) and gill arches (branchiostegal rays removed) (25.6-mm specimen).

TABLE 2. SOME OSTEOLOGICAL CHARACTERS IN *PHENACOBRYCON*, *BRYCONAMERICUS*, *ASTYANAX*, AND *BRYCON*. P = PRIMITIVE, R = REDUCTIVE, L = LABILE, S = SPECIALIZED; SEE TEXT FOR EXPLANATION.

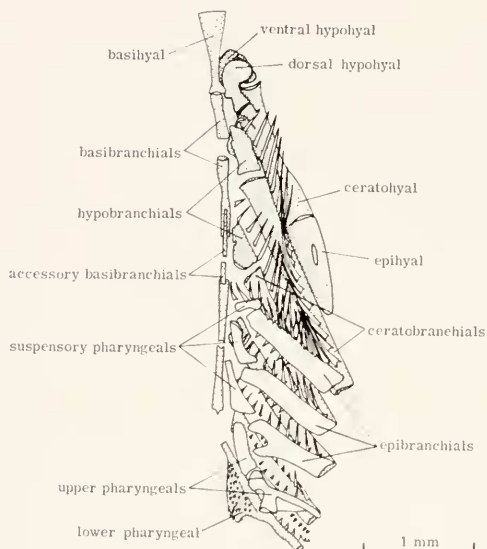|	*Phenacobrycon* (*P. henni*)	*Bryconamericus* and *Astyanax* (*B. brevirostris*, *B. scleroparius*; *A. festae*)	*Brycon* (*B. meeki*, after Weitzman, 1962; *B. dentex*)
1. Supraorbital	absent R	absent R	present P
2. Circumorbitals	1, 2, 3, 4, 5, 6 P	1, 2, 3, 4, 5, 6 P	1, 2, 3, 4, 5, 6 P
3. Rhinosphenoid	absent L	absent L	present P?
4. Posteriorly directed ventral process on orbitosphenoid	strongly developed R?	weakly developed L	absent P?
5. Posteriorly directed ventral pterotic process	absent R	weak R	strong P, L
6. Epiotic bridge	relatively narrow R	relatively narrow R	relatively wide P?
7. Number of tooth rows on premaxillary	2 P	2 P	3 or 4 (irregular rows) S
8. Teeth on maxillary	a single small tricuspid tooth at junction with premaxillary R, L	absent (*Astyanax*); two small tricuspid teeth at juncture with premaxillary (*Bryconamericus*) R, L	13–15 tricuspid teeth extending entire length of descending limb P?, L
9. An internal row of two teeth near symphysis of lower jaw (one tooth on each dentary)	absent R?	absent R?	present P?, L
10. Mode of tooth replacement	alternating from side to side of the jaws P	alternating from side to side of the jaws P	alternating from side to side of the jaws P
11. Ossified basibranchials	1 P, L?	4 P, L	3 L, P
12. Postcleithra	1, 2, 3; 1 and 2 widely separated; 3 with proximal laminar portion P	1, 2, 3; 1 and 2 widely separated; 3 with proximal laminar portion P	1, 2, 3; 1 and 2 in contact (*B. meeki*) or only slightly separated (*B. dentex*); 3 strutlike, without laminar portion P
13. Supraneurals	6–7 R	5–6 R	10 (*B. meeki*), 11 (*B. dentex*) S?
14. Epurals	2 P	2 P	2 (*B. dentex*), 3 (*B. meeki*) P, L
15. Vertebrae	16 + 18 L	16 – 17 + 17 (*Astyanax*); 17 + 18 – 19, 18 + 18 (*Bryconamericus*) L	22 – 23 + 23 S?

Figure 21. *Landonia latidens.* Dorsal view of right half of hyoid (minus interhyol) and gill arches (branchiostegol rays removed) (32.1-mm specimen).
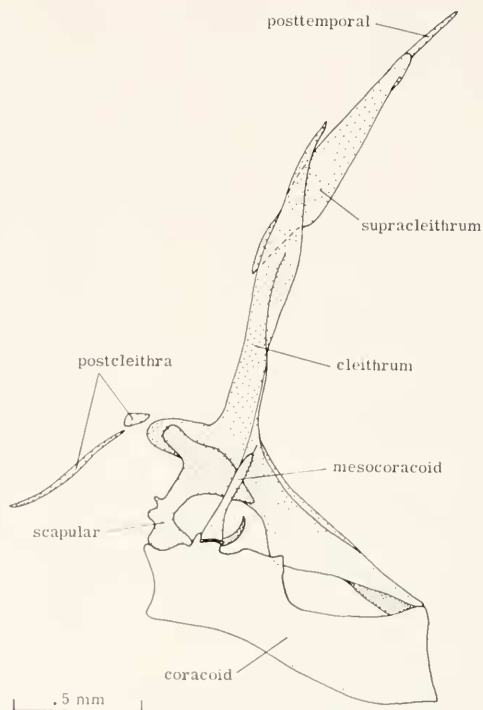

Figure 22. *Iotabrycon praecox.* Internal view of left half of pectorol girdle (17.4-mm specimen).

In all three genera the lateral foramen of the exoccipital is unusually large.

Jaws (Figs. 5, 6, 11–16). The jaws of *Phenacobrycon* (Figs. 5, 13, 14) are similar to the jaws of *Bryconamericus* and *Astyanax.* The dorsal surface of the distal end of the premaxillary is notched to receive the ventral edge of the maxillary's ascending process. This notch is a relatively constant feature in many Tetragonopterinae and other characids with multicuspid teeth. It is present in such generalized forms as *Brycon, Salminus,* and the African genus *Alestes.* In these forms the lateral wall of the notch in the premaxillary bone lies external to the ascending maxillary limb (as in Fig. 13 of *Phenacobrycon*). In *Landonia* the notch is absent, and the entire ascending limb of the maxillary lies external to the premaxillary. This can be seen in Figure 15, a lateral view of *Landonia,* but it is more apparent when the jawbones are viewed from above (not figured).

A second marked peculiarity of the maxillary in *Landonia* is the shape of its

distal end, the trailing edge of which is curved outwards. From manipulation of the alizarin preparations the impression is gained that these peculiarities of the maxillary in *Landonia* are functionally significant in aligning the straight-edged teeth of the maxillary with those on the dentary close enough that their shearing or scissor-like action can be effected. This action possibly could be further enhanced by dilation of the rami of the lower jaws; in *Landonia,* as in *Phenacobrycon* and many other characins, the two halves of the lower jaw are movably joined at the symphysis by a symphyseal hinge joint.

In *Phenacobrycon* the maxillary is moderately long and slender, with a slightly convex ventral margin, similar in shape to the maxillary of *Bryconamericus.* The maxillary of *Astyanax* is relatively short, with its distal end expanded. It may be
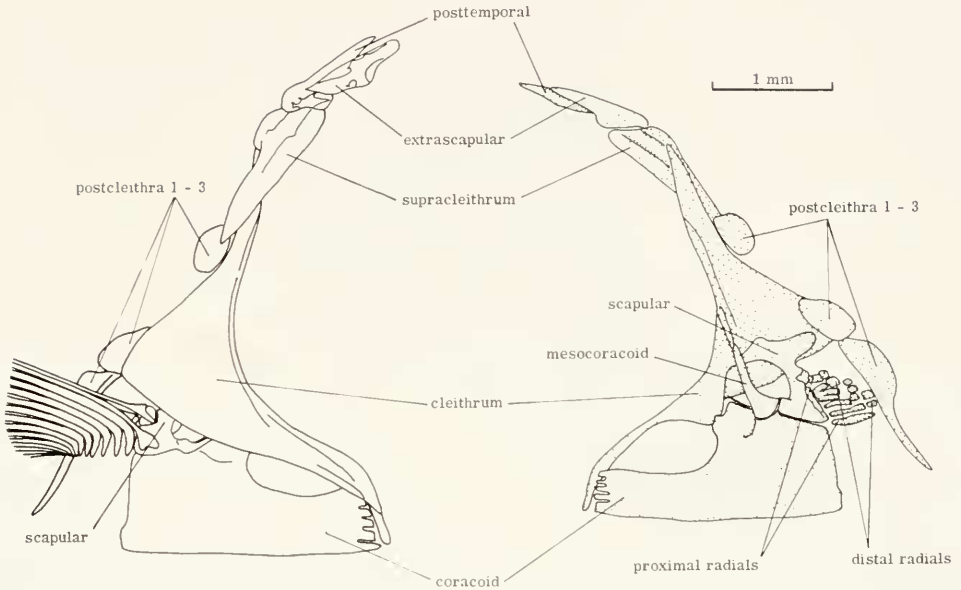
Figure 23. *Phenacobrycon henni.* Lateral and internal views of right half of pectoral girdle (25.6-mm specimen).

noted that the dentary of *Landonia* is relatively elongate, and in this respect more similar to the dentary of *Bryconamericus* than to that of *Astyanax*.

Facial bones (Figs. 11–16). All three genera lack the supraorbital and have a tubular nasal bone and an antorbital bone similar in shape and position to the nasal
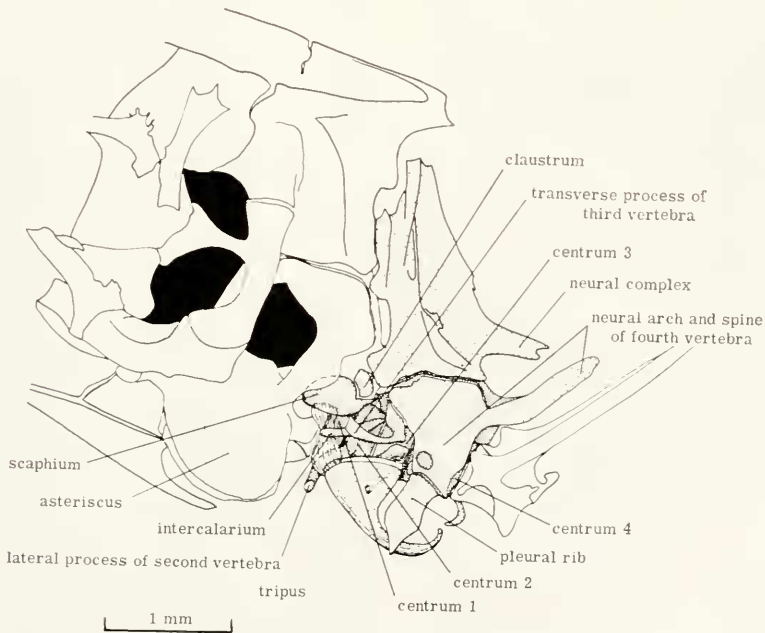

Figure 24. *Landonia latidens.* Lateral oblique view of Weberian apparatus (42.1-mm specimen).
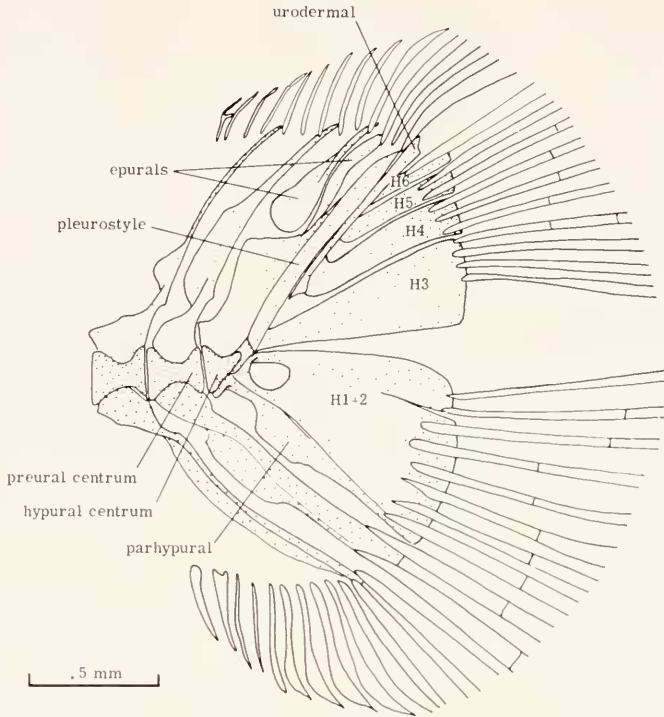
Figure 25. *Iotabrycon praecox*. Lateral view of caudal skeleton (18.8-mm ♂). Note enlarged lower procurrent caudal rays.

and antorbital in *Bryconamericus* and *Astyanax*. *Phenacobrycon* has six infraorbitals, the shape and size of each similar to the corresponding elements in *Bryconamericus* and *Astyanax* (Fig. 13). *Landonia* has but four separate infraorbitals (Fig. 15). The first separate element (= fused first and second infraorbitals?) is elongate; its leading edge is indented, thus permitting the flared distal end of maxillary bone to lie uncovered by it when mouth is closed. The second separate element (= fused third and fourth?) is slightly enlarged compared to corresponding elements in *Phenacobrycon* and *Bryconamericus*. The number and relative sizes of the circumorbitals is the same in all five specimens of *Landonia*. *Iotabrycon* has only three circumorbitals (Fig. 11), the number and relative size the same in the three specimens examined.

The opercle, subopercle, interopercle, and preopercle are similar in size and shape in all three genera and are much as in *Bryconamericus* and *Astyanax*. In *Phenacobrycon* and *Landonia* the dorsalmost part of the preopercular branch of the laterosensory canal system is enclosed in a separate, tubular, bony suprapreopercle.

Visceral arches (Figs. 17–21). The visceral arches are similar in all three genera, the principal difference lying in the numbers of gill rakers. All have a well-ossified fourth basibranchial, thus agreeing with *Bryconamericus* and *Astyanax* but differing from *Brycon*, which has only three ossified basibranchials (excluding "accessory" ossifications).

Pectoral girdle (Figs. 22, 23). The pectoral girdles are virtually identical in *Phenacobrycon* and *Landonia*. The dis-
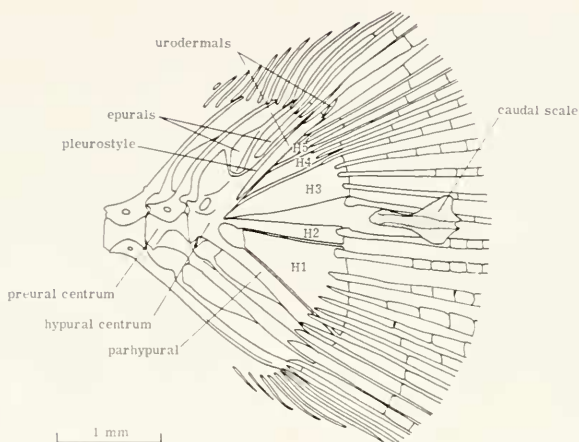
Figure 26. *Landonia latidens.* Lateral view of caudal skeleton and modified terminal scale of pored lateral line series (32.1-mm specimen).

position of the three postcleithra differs from that in *Brycon:* in *Brycon,* the first and second postcleithra are in contact, and the third postcleithrum is strut-like. In *Phenacobrycon* and *Landonia* the first and second postcleithra are widely separated and the proximal half of the third postcleithrum is laminar. *Iotabrycon* differs from *Phenacobrycon* and *Landonia* chiefly in that the first postcleithrum is absent, the second greatly reduced, and the third an elongate strut with no lamellar portion.

In *Iotabrycon* the posttemporal is a simple shaft (absence of lower limb correlated with absence of intercalar). In *Phenacobrycon* the lower limb of posttemporal is short and weakly developed (in one specimen) or absent (in two specimens, including the one on which Fig. 23 is based). In *Landonia* (pectoral girdle not figured) the lower posttemporal limb is moderately well developed.

Pelvic girdle (Fig. 4). The pelvic girdle is similar in all three genera, and like that in other characids which have a generalized pelvic girdle. *Phenacobrycon* and *Landonia* have eight pelvic rays, as have *Bryconamericus* and *Astyanax. Iotabrycon* has only seven. The distribution of hooks on the pelvic fin rays in males differs in the three genera, as discussed above.

Weberian apparatus (Fig. 24). The Weberian apparatus is similar in all three genera and like that of other generalized characids. The scaphium is relatively large in *Iotabrycon,* as is usual in characids of greatly reduced size.

Caudal skeleton (Figs. 25, 26). The caudal skeleton is similar in all three genera, and very much like the caudal skeleton in *Bryconamericus* and *Astyanax.*

Vertebral counts. The total vertebral and precaudal-caudal vertebral counts are very close in the three genera. *Phenacobrycon* has 34 vertebrae (excluding hypural), *Landonia* 35 or 36, and *Iotabrycon* 35 or 36. Frequencies of precaudal and caudal vertebrae were observed as follows: *Phenacobrycon,* 16 + 18 (3 specimens); *Landonia,* 16 + 19 (3) and 16 + 20 (2); and *Iotabrycon,* 17 + 18 (1) and 17 + 19 (2). The similarity of these counts is evidence for relationship, but it must be borne in mind that *Astyanax* and *Bryconamericus* also have vertebral counts similar to these.

DISCUSSION

An attempt has been made in Tables 1 and 2 to evaluate systematic characters according to whether they are primitive,

labile, reductive, or specialized with regard to Tetragonopterinae or generalized characids. Primitive characters (*P*) cannot be used to show relationships when they are common to many forms outside the group being considered. Labile characters (*L*) change readily, often show a mosaic distribution, and are of limited use in determining relationships. Reductive characters (*R*), including loss characters, occur commonly and independently, especially in forms with greatly reduced body size, and are likewise of limited utility. Specialized characters (*S*) are those that are most important in determining relationships. Ideally, specialized characters originate only once, i.e., are incapable of having originated independently. We may note in passing that the generic classification in *The American Characidae* is based largely on reductive and labile characters.

The osteology of what will doubtless prove to be the great majority of species in the subfamily Tetragonopterinae and in the subfamilies derived from it is relatively uniform. This is not difficult to believe when one considers the sameness in habitus and dentition in literally hundreds of species belonging to large genera and groups of genera such as *Astyanax, Bryconamericus, Moenkhausia, Hyphessobrycon,* and *Hemigrammus.* A worker might assume that two characids are closely related because they share osteological features that are truly similar, not realizing that these characters are very widespread. One must use as many osteological characters as possible and even then the results may prove inconclusive. In the present instance I have not been able to find any specialized osteological characters which would serve to identify *Iotabrycon, Phenacobrycon,* and *Landonia* as a closely related group. The osteological characters they share are all generalized and can be found in many other characids, including the non-glandulocaudines *Bryconamericus* and *Astyanax* from the same basin. Thus the osteological characters shared by *Phenacobrycon* and *Bryconamericus* do not prove a close relationship. Most of the osteological differences between *Phenacobrycon, Landonia,* and *Iotabrycon* and between them and such generalized American characids as *Brycon* (Weitzman, 1962), *Bryconamericus,* or *Astyanax,* are related to either 1) modifications of the jaws and jaw teeth or 2) differences in the extent of ossification which are correlated with body size. *Phenacobrycon* and *Landonia* are similar osteologically except for differences in their jaw dentition, ethmoid regions, and circumorbitals.

Of the three Guayas glandulocaudines, *Phenacobrycon* is more generalized than either *Iotabrycon* or *Landonia* in its dentition and possession of six separate circumorbital bones. Compared to *Iotabrycon, Phenacobrycon* is also more generalized in its retention of an adipose fin, complete squamation, and complete lateral line. With respect to *Landonia,* it is also more generalized in its jaw morphology and perhaps in having fewer scales. The similarity in coloration of live specimens reported here may be taken as additional evidence that *Landonia* and *Phenacobrycon* are closely related, as first suggested by Myers (Eigenmann and Myers, 1929: 4). On the other hand, the morphology of the maxillary bone and circumorbital series, complete enclosure of all but the internal premaxillary row of replacement teeth within the jaw bones, and probably the mode of tooth replacement of *Landonia* indicate considerable divergence from its presumed *Phenacobrycon*-like or *Bryconamericus*-like ancestors. *Landonia* is immediately distinguished from all other characids by the morphology of its teeth. The small size of scales in *Landonia* may be an adaptation to lessen autopredation on scales; small scale size and more adherent scales are characteristic of all the characoid genera that are highly specialized as scale-eaters: they tend to feed on fishes with scales much larger than their own (Roberts, 1970). On the

other hand, the dentition of *Landonia* is probably primarily adapted to some other kind of food, and the gut contents of specimens taken during the dry season are probably different from what one would find in the wet season.

Overall, *Iotabrycon* looks modified in a reductive way with unique specialization in the caudal gland. The presence of a rhinosphenoid is a surprise, since all other osteological differences between *Iotabrycon* and *Phenacobrycon* and *Landonia* seem to be those commonly associated with extreme size reduction in Characidae, i.e., failure of the epiotic bone to form a bridge across posttemporal fossa; reduction of circumorbital series; absence of intercalar; conical dentition; and reduction of bony canals enclosing cephalic laterosensory system. The rhinosphenoid occurs in many South American genera of Characidae, and also in Hemiodontidae and Cynodontidae. There is some indication that it has a mosaic distribution. Thus the rhinosphenoid is absent in *Astyanax festae* but present in *Astyanax fasciatus* (MCZ 46756 from the coast of Ceará). The presence or absence of the rhinosphenoid may in some degree be dependent on development of the orbitosphenoid. The series *Bryconamericus–Landonia–Phenacobrycon–Iotabrycon* shows a progressively more developed *orbitosphenoid*. In larval *Brycon dentex* the orbitosphenoid is well developed and ossified before there is any indication of the rhinosphenoid.

Some comments concerning the hooks on the fin rays in males of many New World Characidae are in order. The hooks differ from pearl organs and breeding tubercles in being osseous structures invariably associated with segmented rays rather than keratinous structures of widespread occurrence on the body and fins. The earliest reference to the hooks of Characidae is probably by Jenyns (1842: 126), who distinguished *Tetragonopterus* (= *Astyanax*) *scabripinnis* from other species by the anal fin rays "being set with

asperities, which communicate a scabrous harsh feel to the touch, when the finger is passed along them from the base upwards." He also mentioned the scabrous condition of the anal fin in one specimen of *Tetragonopterus* (= *Cheirodon*) *interruptus* (*op. cit.*, p. 128), and suggested that this may be a sexual character common to several species. The occurrence of hooks was recorded for many species in *The American Characidae* (Eigenmann, 1917–1927; Eigenmann and Myers, 1929). More recent records are reviewed by Wiley and Collette (1970: 164–165). Nelson's remark that "the presence of caudal and even dorsal fin hooks in the male *Acrobrycon* certainly suggests that in that genus fertilization is internal" (Nelson, 1964a: 129) should be questioned. The hooks, which perhaps hook onto the unarmed rays in the female when the fins of a mating pair come in contact, presumably would facilitate spawning accompanied by external fertilization. This is especially so if the action takes place in swift current, as it presumably does in *Bryconamericus* sp. undet. (MCZ 48669), in which well-developed hooks are present on all of the fin rays in all of the fins, including the dorsal and pectorals. One specimen of this form was collected in the Río Toachi, Río Esmeraldas drainage, about 15 km E of Santo Domingo, altitude approximately 900 meters, on 19 October 1971. In this region the river is very swift, and even in the pools, which are scarce, there tends to be considerable current. Böhlke (1958: 12) reported that adult males of *Bryconamericus peruanus* have hooks on all fins supported by rays, but did not indicate locality or habitat whence the specimens came. In lowland populations of *Bryconamericus* "*peruanus*" (= *Bryconamericus scleroparius*) that we sampled the hooks occur only on the anal and pelvic fins. There is no reason to believe that internal fertilization occurs in more than a small proportion of characids having hooks. On the other hand, hooks are probably preadaptive to the evolution of

internal fertilization. At the present time it is premature to state that internal fertilization occurs in all glandulocaudines (see Bussing and Roberts, 1971).

LITERATURE CITED

BÖHLKE, J. 1958. Studies on fishes of the family Characidae—No. 14. A report on several extensive recent collections from Ecuador. Proc. Acad. Nat. Sci. Philadelphia, **110:** 1–121.

BUSSING, W. A., AND T. R. ROBERTS. 1971. Rediscovery of the glandulocaudine fish *Pterobrycon* and hypothetical significance of its spectacular humeral scales (Pisces: Characidae). Copeia, **1971**(1): 179–181.

EIGENMANN, C. H. 1917–27. The American Characidae. Mem. Mus. Comp. Zool., Harvard, vol. 43, pt. 1, pp. 1–102, 16 pls. (1917); pt. 2, pp. 103–208, 22 pls. (1918); pt. 3, pp. 209–310, 28 pls. (1921); pt. 4, pp. 311–428, 24 pls. (1927).

———. 1922. The Fishes of Western South America. Part I. Mem. Carnegie Mus., vol. 10, no. 1, pp. 1–346, 35 pls., 1 map.

———, A. HENN, AND C. WILSON. 1914. New fishes from Western Colombia, Ecuador, and Peru. Indiana Univ. Studies no. 19, 15 pp.

———, AND G. S. MYERS. 1929. The American Characidae. Mem. Mus. Comp. Zool., Harvard, vol. 43, pt. 5, pp. 429–574, 11 pls.

GÉRY, J. 1965. A new genus from Brazil—*Brittanichthys*—a new, sexually-dimorphic characid genus with peculiar caudal ornament, from the Rio Negro, Brazil, with a discussion of cheirodontin genera and a description of two new species, *B. axelrodi* and *B. myersi*. Tropical Fish Hobbyist, February, 1965: 13–14, 18, 20–24, 61–65, 67–69.

JENYNS, REV. LEONARD. 1842. The Zoology of the Voyage of H.M.S. BEAGLE. Part IV. Fish, xvi + 172 pp., 29 pls.

MYERS, G. S., AND J. BÖHLKE. 1956. The Xenurobryconini, a group of minute South American characid fishes with teeth outside the mouth. Stanford Ichth. Bull., **7**(2): 6–12.

NELSON, K. 1964a. Behavior and morphology in the glandulocaudine fishes (Ostariophysi, Characidae). Univ. California Publ. Zool., **75**(2): 59–152.

———. 1964b. The temporal patterning of courtship behaviour in the glandulocaudine fishes (Ostariophysi, Characidae). Behaviour, **24**(pts. 1–2): 90–146.

———. 1964c. The evolution of a pattern of sound production associated with courtship in the characid fish, *Glandulocauda inequalis*. Evolution, **18**(4): 526–540.

ROBERTS, T. R. 1967. Tooth formation and replacement in characoid fishes. Stanford Ichth. Bull., **8**(4): 231–247.

———. 1970. Scale-eating American characoid fishes, with special reference to *Probolodus heterostomus*. Proc. California Acad. Sci., ser. 4, **38**(20): 383–390.

TORTONESE, E. 1941–42. Ricerche ed osservazioni sui Caracidi delle sottofamiglie Tetragonopterinae, Glandulocaudinae e Stethaprioninae (Teleostei Plectospondyli). Boll. Mus. Zool. Anat. Comp. R. Univ. Torino, **49**(ser. 4, no. 117): 11–86, 5 pls.

WEITZMAN, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichth. Bull., **8**(1): 1–77.

WILEY, M. L., AND B. B. COLLETTE. 1970. Breeding tubercles and contact organs in fishes: their occurrence, structure, and significance. Bull. Amer. Mus. Nat. Hist., **143**(3): 143–216.